SOME REMARKS ON THE CYTOLOGY OF OENOTHERA

by

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With 6 textfigures.

Of late the cytology of the genus Oenothera has been repeatedly discussed. Originally the question whether there occurs parasynapsis or telosynapsis in this genus formed the main point of these discussions.

Most investigators described Oenothera as a specimen of telosynapsis (Geerts, Gates, Davis, Cleland, Håkansson, etc. [1]), although from the beginning the opinion of parasynapsis has been maintained by a few others. As early as 1910, Stomps [2]) held the latter opinion regarding Oenothera, this being the result of a comparison between the corresponding stages in Spinacia and the plant under discussion. In later years it was especially Boedijn [3]) who

[1]) Geerts, J. M., Rec. d. trav. bot. néerl., Vol. 5, 1908, p. 93. Gates, R. R., Bot. Gaz., Vol. 43, 1907, p. 81; Vol. 46, 1908, p. 1; Vol. 51, 1911, p. 321. Davis, B. M., Ann. Bot., Vol. 23, 1909, p. 551; Vol. 24, 1910, p. 631; Vol. 25, 1911, p. 941. Cleland, R. E. Am. Jo. Bot., Vol. 57, 1922, p. 391; Am. Nat., Vol. 57, 1923, p. 562; Bot. Gaz., Vol. 77, 1924, p. 149; Am. Nat., Vol. 59, 1925, p. 475; Genetics, Vol. 11, 1926, p. 127; Bot. Gaz., Vol. 82, 1926, p. 55. Håkansson, A., Hereditas, Vol. 8, 1926, p. 255.

[2]) Stomps, Th. J., 1910. Kerndeeling en Synapsis bij Spinacia oleracea. p. 124.

[3]) Boedijn, K., Zeitschr. f. Zellen- u. Gew. lehre, Vol. 1, 1924, p. 265; Rec. d. trav. bot. néerl., Vol. 22, 1925, p. 173.

advocated parasynapsis. The latter studied not so much the praesynaptic stages, but pachynema and diakinesis.

Of late a new aspect in the investigations has presented itself, now that Cleland maintains that there occurs telosynapsis: he gives an entirely different explanation of the following phases. He argues that out of the synaptic knot there appears a single thread, which is gradually thickening and shortening, in this way finally forming a diakinetic stage with a continuous chain of chromosomes, connected to each other by a fine achromatic thread.

He even sees *rings*, the number of chromosomes in each of these rings being a fixed one for a given species. In metaphase Cleland sees that the chain assumes a zigzag arrangement, whereas in the following anaphase he finds that the chromosomes situated next to each other go to the opposite poles. From these facts Cleland concludes that the situation of the chromosomes in the rings is a fixed one.

After Cleland a number of other investigators confirmed his discoveries as to the presence of rings (Håkansson, Kihara, Sinotô, Sheffield [1]).

Valcanover [2]) only mentioned the presence of chains and did not agree with regard to the following metaphase, maintaining that there is a distinct equatorial plate in metaphase. Kihara, on the other hand, tried to explain the formation of rings as a result of parasynapsis, comparing meiosis in Oenothera with that in Rumex acetosella.

Boedijn was the only one who denied the presence of rings or chains, maintaining that after side by side arrangement in synapsis seven pairs of chromosomes come out, which are loose from each other in diakinesis, but will show accidental adherings.

[1]) Håkansson, A. l.c. Kihara, H. Jahrb. f. wiss. Bot., Vol. 66, 1926, p. 429. Sinotô, Y., Bot. Mag. Tokyo, Vol. 41, 1927, p. 225. Sheffield, F. M. L., Ann. Bot., Vol. 41, 1927, p. 779.
[2]) Valcanover, R., La Cellule, Vol. 37, 1926.

My intention now is to state in a few words my own observations concerning these facts, but in due time I hope to be able to publish more eleborate views on the problem. At present I may be allowed to say that I am rather sceptic as to the far-reaching importance of Cleland's observations.

It is, indeed, a fact that chains or rings, may be seen in the diakinesis of a number of Oenotheras, but it is doubtful to me whether there are in a given species rings and chains present, composed of a fixed number of chromosomes. I may already say that in the ovules of Oe. Lamarckiana no chains of a *definite* number of chromosomes are formed, but that the sticking together is rather an accidental occurrence (Fig. 1). *)

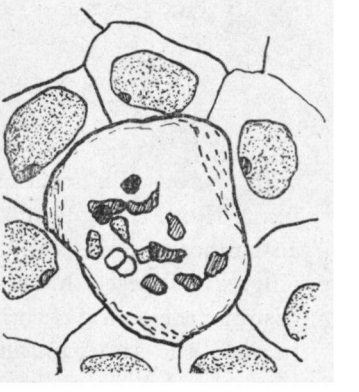

Fig. 1.

My chief objection to the above opinion is that finally in a heterotypic division all chromosomes become loose from each other, and it is decidedly unacceptable that the chromosomes after a fertilization, followed by an entire diploid phase, should arrange themselves in a completely identical order of succession. There is just as much possibility that a former chain AA'BB'CC', etc., may now be arranged A'ABB'CC', or in any other way, provided that the pairs of chromosomes remain together after the pachynema stage.

*) All figures were sketched with the aid of a camera lucida under the Zeiss apochromatic objective 2 m.m. (N.A. 1.3) in combination with the compensating ocular No. 18, giving a magnification of 2250 diameters. The sections were 10 μ thick and stained with iron-alum haematoxylin.

Another objection may be raised against Cleland's principal views regarding the presence of a small number of linkage groups together with an absolute linkage within each group; from the study of my preparations the conviction has grown upon me that Oe. Lamarckiana and Oe. biennis, which have been studied by me, show a clear case of parasynapsis. The fact that parasynapsis occurs in Oenothera deprives Cleland's remarks from the importance which otherwise they would have had.

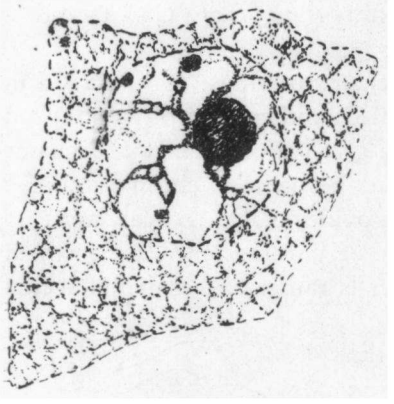

Fig. 2.

In praesynapsis I observe, at least in preparations fixed with Nawaschin solution [1]) or with Gilson-Petrunkewitch fixing fluid, the appearance of delicate threads which display anastomoses and, consequently, gaps in several places. (Fig. 2). These threads are gradually thickening at the cost of the existing chromatic material. Even then there may be seen the said gaps and doublings in the threads (Fig. 3). Later on I hope to be able to give more evidence of the number of these threads: at present it may be only said that this number is certainly less than 14. At any rate there is evidence that the gaps in the threads are not due to a telophasic split in the mitosis preceding meiosis.

Then follows synapsis; when the slides have been far

[1]) The *modified Nawaschin solution,* as it is now applied by a number of Russian cytologists, has the following formula:

Chromic acid 1 %	10 cm³
Commercial formaldehyde	4 cm³
Glacial acetic acid	1 cm³

differentiated it is possible to distinguish 7 thick zygosomes in the late stages of the synaptic knot (Fig. 4, 5). The same

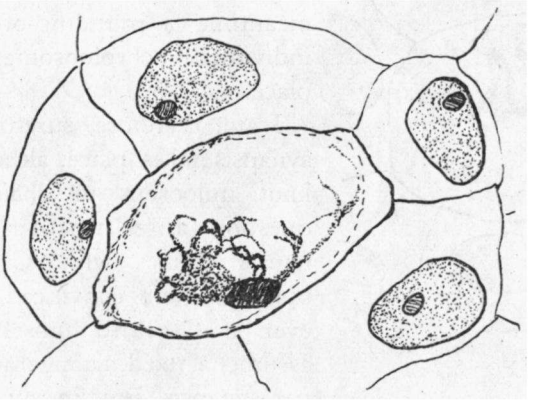

Fig. 3.

thing has already been mentioned by Boedijn [1]).

Out of the synapsis appear a number of thick loops, which occasionally show a double nature (Fig. 6). These loops may loosen with one end from the knot in such a way that in the following phase one may distinguish seven pairs of thick threads, radiating from a centre and sometimes twisted round each other.

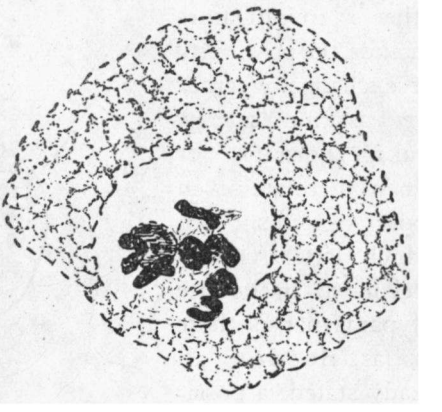

Fig. 4.

Now follows the transition to diakinesis, the pairs mutually adhering and

[1]) Boedijn, K., 1924, l.c.; 1925, l.c.

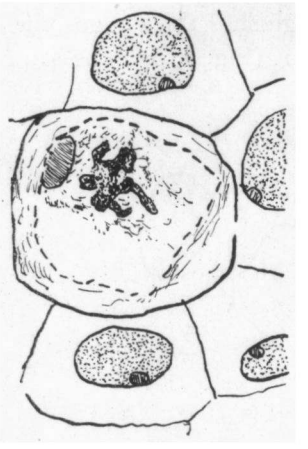

Fig. 5.

becoming attached to the other pairs, so that different types of chains may be formed. In the meantime a rounding-off of the individual chromosomes takes place.

I am, therefore, sure that parasynapsis takes place, although the knot unloosens in chains. The question arises whether parasynapsis clashes with Cleland's opinion. I am convinced it does, even if Cleland himself should assume a fixed arrangement after parasynapsis. But, in my opinion, a side by side arrangement is incompatible with the condition of a few linkage groups going together with the phenomenon of absolute linkage.

My observations on parasynapsis, together with those of other investigators include the possibility of exchange, whether we assume a few linkage groups, or when there are seven loose groups, for which latter view I feel most. In the case of parasynapsis there is, as Boedijn already stated, a possibility of crossing over in early prophase, and we are not compelled to assume an

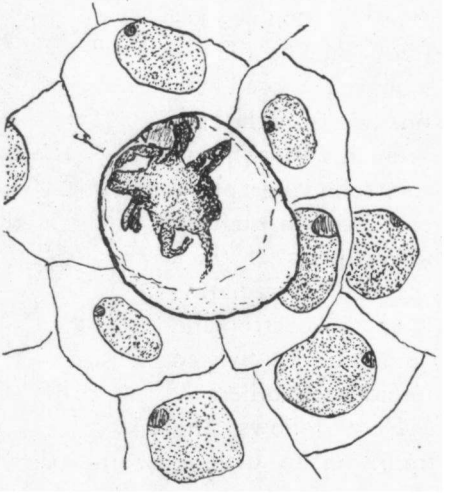

Fig. 6.

exchange of chromatic material in metaphase, or in any other stage where the chromosomes have already been formed.

At any rate Cleland's cytological work is valuable, he being the first who indicated the zigzag arrangement in metaphase, an arrangement which is logically connected with the presence of chains, although in most cases this fact is only evident in a small number of chromosomes, viz. five or seven of them, which may be brought again in agreement with the fact that the forming of chains is accidental.

Explanation of the textfigures.

Fig. 1. Diakinesis in the ovule of Oe. Lamarckiana: 14 chromosomes may be seen, only occasionally showing a connection. Fixation: Nawaschin.

Fig. 2. Praesynapsis in the pollen mother-cell of Oe. Lamarckiana: double threads. Fixation: Gilson-Petrunkewitch.

Fig. 3. Praesynapsis in the ovule of Oe. Lamarckiana: somewhat later stage, the threads thickening and contracting against the nucleolus. Fixation: Nawaschin.

Fig, 4. Late synapsis in the pollen mother-cell of Oe. Lamarckiana: 7 zygosomes, lying in the far differentiated achromatic material. Fixation: Nawaschin.

Fig. 5. Same stage as in fig. 4 in the ovule of Oe. Lamarckiana. Fixation: Nawaschin.

Fig. 6. Pachynema stage in the ovule of Oe. biennis: 7 double threads are visible, loosening from the knot. Fixation: Nawaschin.